Ecological Factors on Manana Island, Hawaii

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ABSTRACT: A 25-ha islet occupied by seasonally nesting sea birds, feral rabbits, and house mice is considered. Rabbits presumably modified the unknown original vegetation in their 70 or more years on the island and reached an equilibrium with a plant cover composed largely of a few hardy introduced grasses. A total of 28 species of higher plants has been recorded from the island, only 6 of which are native to Hawaii. Rabbits occur in low to moderate numbers, sustained by a food source that is enriched by bird guano and subject to annual drought. Average body weight of the mouse is remarkably heavy at 19.5 g. Data on biological and food habits are presented for both mammals. Among 13 species of ectoparasites of birds and mammals are two unusual host adaptations: of the cat flea, *Ctenocephalides felis felis,* to *Oryctolagus cuniculus,* and of the Oriental rat flea, *Xenopsylla cheopis,* to *Mus musculus*. Rabbits appear not to be detrimental to the nesting of birds, and their control or extermination is discouraged at present. The scientific importance of the island's unique ecosystem is stressed, and proposals for its intensive study are outlined.

Most of the lands in Hawaii were altered rapidly, in the hundred years or so following initiation in 1778 of sustained contact with outside cultures, through agricultural development and the spread of introduced plants and herbivorous animals. Then there came a period of lessened disturbance simply because purposeful exploitation of land was diminished and because controls were exercised over some major pest species. In the past 50 years, many new balances have emerged among lands, plants, and animals. However, Hawaii is now in a second era of resource development that threatens to overrun not only the lands touched little or not at all by earlier disruptions, but also those which have achieved new levels of ecological stability. This is a universal problem that is not peculiar to Hawaii. Its solution lies in the exercise of wise resource development based on present, as well as future, needs. Lands with prominent natural attributes often serve their highest use only when left undisturbed. Proposals for their manipulation should be preceded by careful study of each individual case.

This paper is concerned with Manana (Rabbit) Island which lies about 1.3 km off the southeast tip of Oahu, Honolulu County. Its principal occupants are a depauperate flora, large numbers of seasonally nesting sea birds, a colony of feral rabbits, and house mice. Since 1945 this island has been a Territorial and State bird reservation whose security from unauthorized landings is now vested in the State Department of Land and Natural Resources. The basis for this status is that Manana has been one of the main nesting grounds for the Noddy Tern, *Anous stolidus* (L.), and the Sooty Tern, *Sterna fuscata* L., two species highly valued by fishermen in locating schools of aku, *Katsuwonus pelamis* (L.), the principal commercial fish of Hawaiian waters. The terns and aku prey on the same species of forage fish, crustaceans, and squids (Gosline and Brock, 1960).

Some ornithologists and conservationists have recommended destruction of the rabbits on Manana as an undesirable invader, in an attempt to enhance and possibly enlarge the colonies of terns and other birds, notably the Wedge-tailed Shearwater, *Puffinus pacificus* (Gmelin). In 1962 a program of rabbit extermination was

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initiated, and poisoning and shooting were carried out on several occasions. For lack of manpower and at the request of interested parties the program was discontinued in 1964.

The purposes of this paper are to review the biological history of Manana, to present some new data on its plant-animal relationships, and to outline a possible course for determining what management practices, if any, should be applied to the island—specifically, whether or not the program of rabbit extermination should be renewed. Principal objections to a policy of rabbit extermination at this time are that little if any evidence is available to show that bird-rabbit relationships are other than harmonious, and that the rabbit in many generations of survival under restrictive conditions has earned a place in the Hawaiian fauna as a resource of importance to science (Tomich, 1965).

As a first step in the project, the authors were permitted to join an expedition to Manana on February 29–March 1, 1964 led by D. H. Woodside of the State Division of Fish and Game. This brief trip allowed some insight into the present status of the vegetation, the vertebrate fauna and certain parasitic elements of Manana ecology. Additional data were gathered on trips to the island by Lamoureux in October 1953 and March 1955, and by Wilson in July 1963, and from interviews with D. H. Woodside and others.

HISTORICAL ASPECTS

Manana is an ancient tuff cone, 25-ha in area (Fig. 1). In the northwest sector of the island is a shallow crater whose broad floor is some 20 meters above sea level. The crater rim is low on the northwest side but rises to a peak of 110 meters on the southeast side. In the northeast sector a remnant of a second crater opens to the sea on the east side. Its bottom contains a series of tide pools. Seaward slopes of Manana vary from low beach terraces to

Fig. 1. Manana Island as seen from the east. Coconut palms (*Cocos nucifera*) and low vegetation are visible in the main crater at right. (Photo by U. S. Marine Corps, January 1966.)

high precipitous cliffs. The southerly outer slopes of the main cone have been eroded into several steep valleys, presumably by intermittent streams. Bryan (1935) and Richardson and Fisher (1950) have given brief but detailed descriptions of the island. Its physical features have not changed appreciably in historic times. The island has suffered few attempts by man to use or modify it for his own purposes. However, the introduction of rabbits at some unknown date prior to 1900 and the establishment of exotic species of plants have undoubtedly changed the original vegetation. In World War II Manana was used as a bombing and strafing target (Green, 1942). Small shells are still found occasionally in its loose soils, although the Navy Department has made some effort to remove these potentially dangerous missiles (Woodside, personal communication).

Because of its easy access, Manana may have been occupied frequently as a fishing station by the Hawaiians. Records of visits for the purpose of studying the flora and fauna are relatively few. Bryan (1935) reported on insects, vegetation, and miscellaneous topics; Munro (1945, 1950) briefly described the vegetation. Richardson and Fisher (1950) made repeated observations on its birds for nearly two years, and also published a list of plants. Other notes, mainly on birds, have accumulated over the years from the excursions of the Hawaii Audubon Society and have been published in their official journal, the Elepaio.

FLORA AND VEGETATION

Collections of plants made on Manana on several occasions provide some information on changes in the flora during the past 40 years (Table 1). A thorough search of the Bernice P. Bishop Museum herbarium has revealed no specimens from Manana collected earlier than 1927; therefore no record is available of the island's flora before the introduction of rabbits. The earliest published information was supplied by Bryan (1935). He reported that Marie C. Neal had compiled a list of 21 species of higher plants from Manana during four trips up to August 1934, but he mentioned only 8 of these species by name in his account. However, 18 species are represented in the 1930 and 1934 collections.

In all, 28 species of higher plants have been found growing on Manana, and at least 18 of these were present at the time of our survey in 1964. Richardson and Fisher (1950) reported only 7 of these 28 species. It is likely that others were actually present, for they did not consider their list as necessarily complete. Of the 7 plants listed for 1950, none is a native Hawaiian species, while 3 of the 18 found in 1964 are native.

Munro (1945, 1950) discussed conditions on Manana between 1937 and 1941, and noted that the soils which have developed on the western slopes of the island and on the crater floor supported a "heavy cover" of introduced grasses and weedy herbs. He noted that the coconut trees were very small in 1941, but he did not give the date of planting. Richardson and Fisher (1950) indicated that the vegetation began to dry up in late May or early June, and by July all the vegetation was "brown and sear."

The most heavily vegetated parts of the island in 1964 were the floor of the main crater and the outer gentle slopes on the southwestern side of the island. In both places a fairly deep rich soil has developed from the decomposed tuff mixed with guano. On the upper south slopes, the upper inner slopes of the main crater, and the outer slopes on the north, east, and west, little or no soil has accumulated except in scattered pockets and cracks in the tuff, and few plants are present. The failure of soil to develop on these slopes is probably related to their steepness and their exposure to strong trade-winds. As the tuff decomposes in these areas, it falls or is blown away, either to lower vegetated areas or into the sea.

The vegetation of the crater floor (Fig. 2) consisted mainly of *Trichachne insularis,* a bunch grass about 1 meter tall, and *Nicotiana tabacum,* an erect herb from 1 to 2 meters tall. Scattered here and there were *Lycopersicon esculentum, Ageratum conyzoides, Boerhavia diffusa, Setaria verticillata,* and *Cenchrus echinatus.* A few plants of *Portulaca oleracea* were found in the eastern portion of the crater floor, and one large shrub of *Sida cordifolia* grew near the northern edge of the crater floor. About 30 trees of

TABLE 1

VASCULAR PLANTS RECORDED FROM MANANA ISLAND, HAWAII[1]

SPECIES	1927	1930	1934	1936	1937	1950	1955	1964
GRAMINEAE								
Cenchrus echinatus L.		X	X	X		X	X	X
Chloris inflata Link			X	X		X	X	X
Cynodon dactylon (L.) Pers.		X						
Dactyloctenium aegyptium (L.) Richt.							X	X
Eragrostis tenella (L.) Beauv. ex R. and S.			X	X				
**Heteropogon contortus* (L.) Beauv.	X	X	X	X			X	
**Panicum torridum* Gaud.		X		X				
Setaria verticillata (L.) Beauv.				X			X	X
Trichachne insularis (L.) Nees						X	X	X
CYPERACEAE								
Cyperus javanicus Houtt.		X	X					
PALMAE								
Cocos nucifera L.						X	X	X
CHENOPODIACEAE								
Atriplex semibaccata R. Br.				X		X	X	X
NYCTAGINACEAE								
**Boerhavia diffusa* L.		X					X	X
PORTULACACEAE								
Portulaca oleracea L.		X	X	X		X	X	X
PAPAVERACEAE								
**Argemone glauca* Pope		X						X
LEGUMINOSAE								
Prosopis pallida (Humb. et Bonpl. ex Willd.) HBK.								X
Tephrosia purpurea (L.) Pers.		X	X	X			X	X
EUPHORBIACEAE								
Euphorbia hirta L.		X		X				
MALVACEAE								
**Sida cordifolia* L.								X
STERCULIACEAE								
Waltheria indica L.		X	X	X			X	
PRIMULACEAE								
Anagallis arvensis L.		X						
BORAGINACEAE								
**Heliotropium curassavicum* L.				X				
SOLANACEAE								
Lycopersicon esculentum L.		X	X				X	X
Nicotiana tabacum L.		X	X	X		X	X	X
CUCURBITACEAE								
Cucurbita pepo L.					X			
COMPOSITAE								
Ageratum conyzoides L.		X		X				X
Pluchea odorata (L.) Cass.								X
Sonchus oleraceus L.		X			X			X

[1] Collections made by: H. A. Lee, 1927; M. C. Neal, 1930, 1934; E. H. Bryan, Jr., 1934; F. R. Fosberg, 1936; F. A. Egler, 1937; C. H. Lamoureux, 1955, 1964; C. R. Long, 1964.

Symbols used: *, Native Hawaiian species.
X, Specimens available.
X, Species cited in literature (for 1934: Bryan, 1935; for 1950: Richardson and Fisher, 1950).

FIG. 2. View toward east across the main crater of Manana Island. Sourgrass (*Trichachne insularis*), wild tobacco (*Nicotiana tabacum*), and coconut palms (*Cocos nucifera*) are prominent components of the vegetation. (Photo by K. Wodzicki, February 29, 1964.)

Cocos nucifera, some as tall as 8 meters, grew on the crater floor, and many of these were producing fruit in 1964.

The vegetation of the outer southwestern slopes (Fig. 3) differed from that in the crater. The dominant plants were *Setaria verticillata* and *Cenchrus echinatus,* mostly 0.5 meter or less in height. Occasional shrubs of *Tephrosia purpurea* occurred here, along with several plants of *Boerhavia diffusa.* Scattered clumps of *Chloris inflata* were found also on these slopes; *Nicotiana tabacum* was occasional. Toward the lower part of the slopes *Atriplex semibaccata* was abundant. Two trees of *Cocos nucifera* grew on the western part of these slopes.

Dactyloctenium aegyptium was restricted to the sandy beach at the base of the slopes. One tree of *Prosopis pallida* was growing high up in the largest valley on the south side of the island. In this same valley were several flowering plants of *Argemone glauca,* and seedlings of this species were found also on the beach at the mouth of the valley.

One mature shrub and a few seedlings of *Pluchea odorata* were found in soil pockets just below the crater rim on the outer southwest slopes, and a few plants of *Sonchus oleraceus* grew in soil pockets on the crater rim.

MAMMALS

Oryctolagus cuniculus

The principal resident vertebrate of Manana is the European rabbit, *Oryctolagus cuniculus* (L.). Identification is confirmed by a flat skin and skull in the Bishop Museum, collected August 27, 1934 by E. H. Bryan, Jr., by two fresh specimens collected by State Fish and Game personnel on August 31, 1961 and examined by K. Wodzicki, and by a series of seven museum specimens prepared from material collected on the 1964 expedition.

The population probably has descended from one or more importations of mixed domestic breeds of several colors. Escaped or planted stocks of domestic rabbits sometimes revert in coloration to the wild type (Thomsen and Evans, 1964), and this is apparently the case with the population on Manana. It now resembles the wild European rabbit, which has

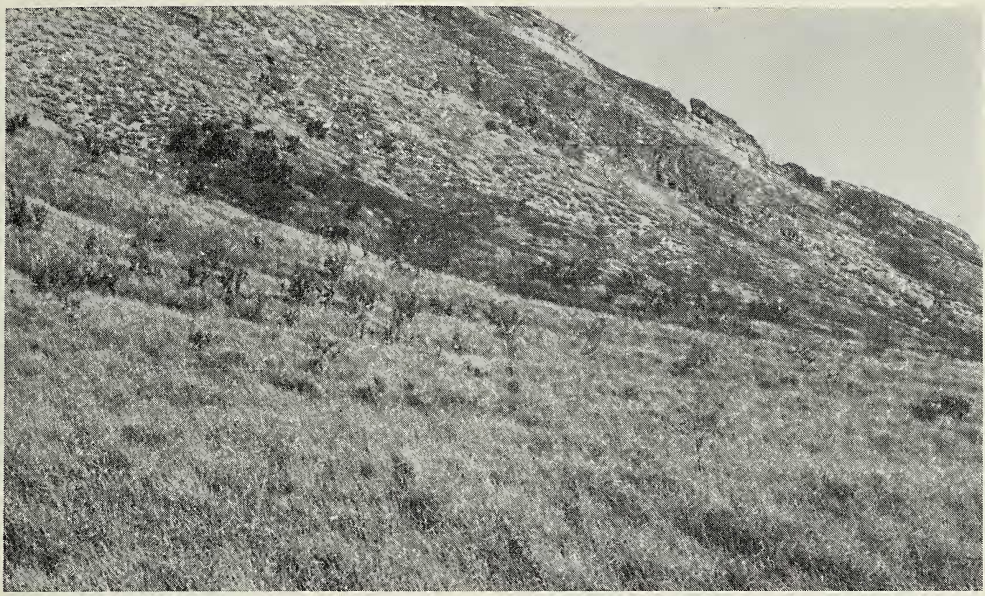

Fig. 3. Outer southwest slopes of Manana Island. Dominant grasses are sandbur (*Cenchrus echinatus*) and bristly foxtail (*Setaria verticillata*); shrubs include ahuhu (*Tephrosia purpurea*) as dark patches in middleground, and wild tobacco (*Nicotiana tabacum*) scattered in foreground. (Photo by K. Wodzicki, February 29, 1964.)

typically an agouti dorsal color with reddishness behind the ears. The throat puff and lower abdominal patches are buff-colored; ventral parts, inclusive of the tail, are otherwise generally white (Fig. 4). However, traces of domestic color traits are still evident in the rabbits on Manana. One of the 1961 specimens was a male with patches of white on both forelegs. Of 13 rabbits examined in 1964, 2 males had similar markings: one a white paw (Fig. 5) and the other an entire white foreleg. These appear to be expressions of the genetic Dutch pattern.

Rabbits have been on Manana for 70 years and perhaps longer. One anonymous writer (1901) stated that, "A few of the small rodents (sic) were taken there many years ago by some party or parties unknown and now they are innumerable." There have been reports in the literature suggesting that species other than *Oryctolagus cuniculus* may have been introduced to Manana, but none of these reports is well founded in fact. W. A. Bryan (1915) listed the rabbit under the misnomer of *Lepus,* the genus of hares, but perhaps properly referred to the animals as a "mongrel breed." De Vos et al. (1956) quote a letter from Ernst Schwarz to the effect that, "A hare, believed to be of Russian origin (species unknown), is found . . . off Oahu." A partial source of Schwarz' information may be Bryan's notation of *Lepus*. Watson (1961) states, "The Manana rabbits closely resemble the American cottontail in color and ear length and it is conceivable that these rabbits are in fact cottontails (*Sylvilagus* spp.)." The source of his information is not given; however, it is known that Watson did not see the rabbits himself.

Several brief notes record the status of the population through the years. The anonymous writer (1901) reports that, as he approached Manana by boat, "Almost every foot of the ground is seen to be occupied by a rabbit; in fact, it is one of the most thickly populated rabbit colonies in the world. . . . They have so denuded the place of all edible vegetation that they are obliged to subsist on small shell fish which they find along the beach. . . . Mr. John Cummins has several hundred of them killed off every year, the meat being salted down and eaten as required."

W. A. Bryan does not indicate whether his report in 1915 that Manana was thickly populated with rabbits was the current condition, or

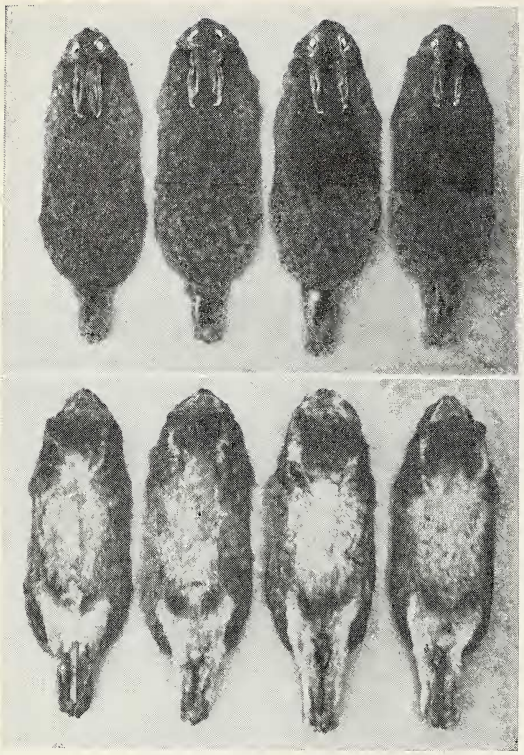

FIG. 4. Dorsal and ventral views of two adult female (*left*) and two adult male (*right*) *Oryctolagus cuniculus* collected February 29, 1964, on Manana. (Photo by P. Q. Tomich.)

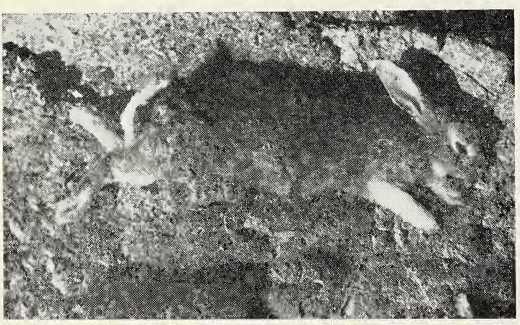

FIG. 5. Freshly shot rabbit from Manana showing wild-type pelage except for white foreleg. Notebook is 18 cm in length. (Photo by K. Wodzicki, March 1, 1964.)

whether he was merely paraphrasing the 1901 statement. A few years later, rabbits may have been plentiful because a note from the Territorial Division of Forestry (Anon., 1919), which apparently had charge of the island then, said, "In March, 1918, 3 chauffeurs were arrested for going to Manana and killing rabbits without a permit. . . ." E. H. Bryan, Jr. records 3 rabbits seen on the August 25–26, 1934 expedition and that they were seemingly in good condition. Vegetation at that time was considered doing well. The next report is by Richardson and Fisher (1950) who made 14 half-day trips to Manana between October 1946 and August 1948. They saw from 2 to about 30 rabbits per trip, with the maximum number observed in June 1948. Wodzicki notes (in litt.) that on August 31, 1961 the landing on Manana was made for about an hour at mid-day, and 5 or 6 rabbits were seen, including the 2 collected. On October 27 of the same year, 15 rabbits were shot as a part of the extermination program (Woodside, personal communication). These scattered records indicate a large early rabbit population on Manana and later populations stabilized at low to moderate levels.

On the February 29–March 1, 1964 trip, rabbits were seen commonly. As the party climbed into the main crater at 4:30 PM, several rabbits were on the dry grassy slope above the beach. Two hunters moving in advance shot two of them among the tobacco plants. Here, as within the crater, the rabbits had burrowed in the friable soil. There seemed to be no distinction between old burrows seasonally used by various birds and those used by rabbits. Thousands of prenesting Sooty Terns milled day and night over the island. At night small numbers of them, as well as of Wedge-tailed Shearwaters, settled, and some were banded by a party of ornithologists also visiting the island. In the crater, by 6:00 PM, the hunters shot and recovered 11 more rabbits. Each person who entered the crater reported seeing several rabbits, in spite of the shooting. Here the vegetation was still quite green, and *Trichachne insularis* was seeding heavily. After dark only a few rabbits were noted, even with the aid of lights. The population for the island may have been as many as 100 juveniles and adults. This would be a fairly large number to be supported by the vegetation, which covers about 10 ha. Heavy rains later in March were effective in extending the growing period into summer, and thus replenishing the food supply.

Rabbit pellets were noticeably scarce on February 29, 1964, in relation to the observed abundance of rabbits. Pellets found, except for

the occasional fresh deposit, had a roughened and weathered appearance. These phenomena were explained when we observed at night that the cosmopolitan terrestrial isopod, *Porcellio laevis* Latreille, swarmed over the rabbit pellets and fed on them. Often a single pellet had several *Porcellio* on it and was rolled about as the isopods shifted position. Thus the destruction of rabbit feces is hastened and the usual methods of censusing rabbits by pellet counts cannot be applied to the Manana population.

Three male body weights were 2189, 1695, and 1670 g and three females weighed 2055, 1970, and 1640 g, indicating a similar weight in the two sexes. Average weight for the six rabbits was 1870 g. Paunched weight averaged 73.6% of the live weight. A male and female collected in August 1961 weighed 2284 and 2087 g, respectively. Paunched weight averaged 70.4% as heavy. Both were fat, rating at 3 and 2, respectively, on a scale of 0 (none) through 3 (heavy). The rabbits observed in 1964 were in good flesh but not fat. On the same scale a pregnant doe registered 1, and four others 0 for an average of 0.2. Five males were 1 and one was 0, for an average fatness of 0.8.

The population had just passed a peak of reproduction. All five adult does were lactating, averaging 2.2 on a scale of 0 through 3. One doe was about 10 days pregnant and showed the least mammary tissue (rated at 1). Corpora lutea were counted easily in the pregnant doe as 8R-1L. Eight embryos were implanted in the right uterine horn, none in the left. Another doe had distinct black uterine scars 4R-0L and corpora lutea 7R-1L, suggesting a 50% preimplantation or early resorption loss. No other scars were found. Uteri of the four parous does definitely were inactive as flabby flattened structures 5 to 7 mm wide. The reproductive rate was seemingly high. These data on corpora lutea, embryos, and placental scars show that litter size may average about 6.0 (allowing for a 25% loss before birth of shed ova and early-stage embryos).

The testes of one adult male weighed 2.7 g and the cauda epididymides had visible tubules indicating the presence of sperm. In another buck testes were larger than this, in two they were of similar size, and in two they were smaller. At least four and perhaps all of the six males were in breeding condition. Regression may have been in progress. That the four parous does were sexually inactive suggests that the breeding season was nearly terminated. Each of the party who crossed the crater reported seeing small young rabbits. The smaller of two juvenile females collected weighed 352 g and was still nursing, for it had a small mass of curds in the stomach.

Age structure offers some clues about the population. Of 12 rabbits classified by age, 5 were less than 10 months old (2 were juveniles), 5 were from 15 to 26 months, and 2 were 33 to 38 months. The criteria used were those of Taylor (1959) which employ the progressive closure of skeletal epiphyseal sutures. These three age groups are spaced at approximately yearly intervals and imply that breeding may normally occur yearly in a season extending from November to April. A rabbit attains adult size at the age of 4 to 5 months.

Because the rabbits on Manana must depend on the few foods available, it is almost mandatory that they eat all palatable plants within reach. The rabbits taken in 1964 all had full intestinal tracts. Reingestion, as described by Meyers (1955) and by Rowley (1956), was evidenced by soft pellets which made up 10% to 40% of the stomach contents of at least seven rabbits. None had other than hard rectal pellets, showing that reingestion takes place earlier in the day than the 4:30 to 6:00 PM period in which the rabbits were shot.

Thorough mastication and the second passage of food through the alimentary canal usually makes identification of food items a tedious process requiring specialized techniques. We were fortunate to have collected a male (2759)[4] which had lost its fourth and fifth upper cheek teeth on one side, resulting in malocclusion and uneven wear of all other cheek teeth. He swallowed most of his foods whole, allowing their easy identification (Table 2). Comparative data for the other rabbits are given in Table 3.

Grass fragments composed over half the identifiable materials in all seven animals, although volumetric measurements were not

[4] All mammal specimen numbers refer to the catalog of P. Q. Tomich.

TABLE 2

FOOD ITEMS IN STOMACH OF RABBIT 2759 WITH POOR DENTAL OCCLUSION, FROM MANANA ISLAND, HAWAII

PLANT	PARTS EATEN	% BY VOLUME
Atriplex semibaccata	Leaves and stems	18
	Seeds in utricles	27
Nicotiana tabacum	Whole flowers, leaf fragments	30
	Seeds and parts of capsules	3
Grasses	Leaves and stems cut in 5–10 mm lengths	15
Lycopersicon esculentum	Whole fruits, pulp, seeds, and skins	7
Portulaca oleracea	Seeds	trace
Total		100

TABLE 3

FOOD ITEMS IN STOMACH AND RECTAL PELLETS OF SEVEN RABBITS WITH GOOD DENTAL OCCLUSION, FROM MANANA ISLAND, HAWAII

ANIMAL NO.	FOODS IDENTIFIED
2754	Grass stems and leaves
2755	Grass fragments; *Portulaca oleracea* leaves
2756	Grass fragments; *P. oleracea* leaves; *Lycopersicon esculentum* leaves
2757	Grass fragments; *Nicotiana tabacum* seeds; *Atriplex semibaccata* fruits
2758	Grass fragments; *L. esculentum* leaves
2760	Grass fragments; *N. tabacum* seeds; *P. oleracea* seeds
2761	Grass fragments; *P. oleracea* leaves

made. This is in contrast with rabbit 2759, in which grasses comprised only 15% of the stomach contents on a volumetric basis. There seem to be at least two explanations for these differences. Animal 2759 may have had different food preferences because of the poor condition of his teeth, or may have eaten less grass than the other animals because of his possibly restricted range on the outer slope of the island. He appeared undernourished but not thin; prepared skeletal parts were fat-free compared to those of six other rabbits, and in flexing the thawing body for skinning, two legs were broken under little pressure. This was the oldest rabbit examined and probably an outcast who never ventured onto the main crater floor. Mykytowycz (1964) reports well-defined territoriality in the wild rabbit as well as a social heirarchy among males. On the other hand, grasses have many thick-walled lignified cells which are not digested readily, and are more likely to pass through the intestinal tract than such thin-walled unlignified materials as tomato fruits and tobacco flowers. Rabbit 2759 was able to digest little of its poorly chewed food, for the rectal pellets contained seeds of salt bush, tomato, tobacco, and purslane, as well as large pieces of grass stems, tobacco capsules, and tomato skins—virtually all the items eaten, except for tomato fruit pulp and tobacco flowers. Rabbits with good occlusion have reasonably complete digestion of many food materials other than grass fragments, so that recovered materials are often mostly grass fiber. Perhaps a combination of differences in local availability of foods and inefficiency of their use account for the differences in food residues between rabbit 2759 and the others. Animal 2757, a female, was the only other rabbit in which salt bush was identified. She was the other member of the 33- to 38-months age class.

Most fragments of grass could not be identified as to genus, but those which could be identified proved to be either *Cenchrus* or *Trichachne.* These were the two most common species on Manana at the time of the study, and unless there is great preferential feeding by the rabbits, one would expect them to occur most commonly in the food materials sampled.

Munro (1950) reported that rabbits on Manana were eating roots of *Boerhavia tetranda* (= *diffusa*). This plant has a large fleshy taproot which is a good source of food, but no identifiable fragments of it were recovered from the rabbits we studied. However, such material probably would be digested readily and would be difficult to detect. Rabbits had gnawed the bark from some erect woody stems of *Nicotiana tabacum* and had also scratched the soil from some of the plants, baring the roots which were then gnawed (Fig. 6).

Aside from *Atriplex semibaccata,* which grew only on the lower, outer slopes of the main

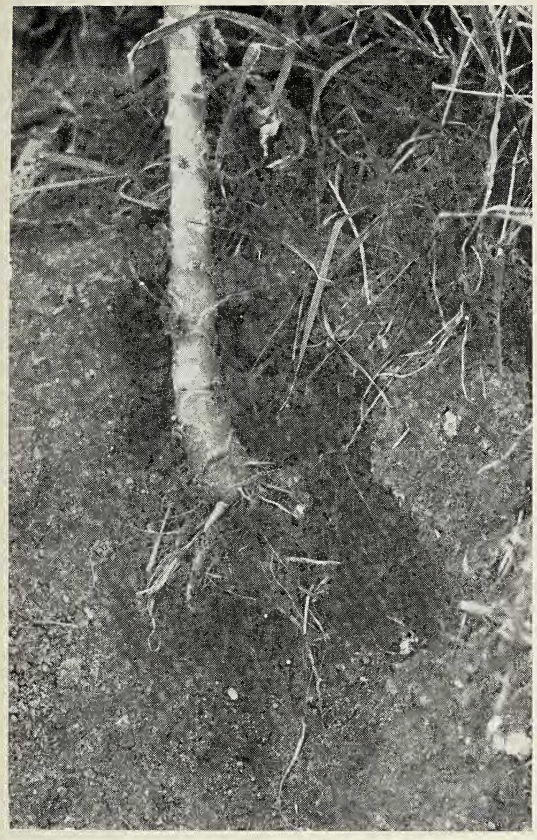

Fig. 6. Wild tobacco plant (*Nicotiana tabacum*) on Manana with bark gnawed, and roots exposed and eaten, by rabbits. (Photo by K. Wodzicki, February 29, 1964.)

crater, all foods identified from each rabbit examined were available to rabbits living in any of the vegetated parts of the island. However, there are differences in abundance of the food plants; for example, *Trichachne insularis* is very common within the crater, but uncommon on the outer slopes. We suspect that the rabbit population is more concentrated in the heavily vegetated main crater than in any other part of the island, and that individually the rabbits may be quite localized. Shifts in range, with the rise and recession of forage plants and of number of rabbits, are quite likely.

Mus musculus

The house mouse, *Mus musculus* L., is the only other mammal on Manana. Rats are not now present and never have been reported. Mice possibly have inhabited the island longer than rabbits, through early accidental introduction by Hawaiians. Tinker (1938) was apparently the first to report *Mus* on Manana, but he offers no detailed information. Richardson and Fisher (1950) briefly discuss this species.

On February 29–March 1, 1964, we found mice commonly active in late afternoon and at night along the beach, on the slopes above the beach, and in the main crater. Fifteen traps set overnight caught three mice, and three others were caught easily by hand at dusk and at night. Mice seen in full daylight early in the morning were noticeably wary.

One mouse was a juvenile weighing 5.4 g; the others were adult. A male weighed 20.0 g, and three females were 22.4, 18.2, and 17.3 g, for a mean weight of 19.5 g (the fifth adult was partly eaten by ants). These are remarkably large mice for Hawaii. For example, on the island of Hawaii adults range generally from 9 to 14 g, and seldom reach 17 g (Tomich, unpublished). A parallel case is reported by Berry (1964) in Scotland.

Reproductive data on the mice from Manana were as follows. The male was in breeding condition, three females were lactating and one female was parous-inactive. One had just borne a litter, as was shown by six prominent uterine scars; another was in estrus. From this small series, it appears that reproduction was at a high level in a mature population, and that weanling offspring were just appearing above ground. Two museum specimens were preserved.

The stomach contents of six mice were examined but identification of foods was difficult. Because of thorough mastication and digestion, very few recognizable fragments remained (Table 4). It was not possible to estimate relative volumes of different foods consumed, nor to compile a list of all materials used by the mice. We conclude, however, that the mice tend to subsist on foods such as seeds, fruits, and insects rather than coarse bulky stems or leaves.

ECTOPARASITES

Parasites of isolated animal populations are expected to be few in number of species be-

TABLE 4

FOOD ITEMS IN STOMACHS OF SIX MICE FROM MANANA ISLAND, HAWAII

ANIMAL NO.	FOODS IDENTIFIED
2746	*Nicotiana tabacum* seeds
2747	Grass stems, leaves, and fruits; insect fragments
2748	*N. tabacum* seeds; grass fruits
2749	*Atriplex semibaccata* fruits and bracts; anthers of grass flowers
2750	*N. tabacum* seeds
2751	*N. tabacum* seeds

cause host chains are often incomplete and the colonizing stock may have been relatively parasite-free. In spite of these limitations, remarkable adaptations may occur if a parasitic species is pressed for survival. Such adaptations are found among the ectoparasites of birds and mammals on Manana. A total of 13 species are recorded, with two collections of Mallophaga from birds identified only as to genus. Of these, 6 species are primarily parasites of mammals and 7 are primarily parasites of birds. The ectoparasites of mammals are much better known than those of birds because the two species of mammals have been examined more thoroughly than the numerous species of birds.

DIPTERA

HIPPOBOSCIDAE

Olfersia aenescens C. G. Thomson

6 ♀ ♀, ex *Anous stolidus* and/or *Sterna fuscata,* July 17, 1963

1 ♀, ex *Oryctolagus cuniculus,* Feb. 29, 1964

This hippoboscid is a common parasite of oceanic birds of the families Phaethontidae and Sulidae (Pelecaniformes) and Laridae (Charadriiformes). There are previous records of this species from Manana, and the specimen reported by Bryan (1935) as *Olfersia spinifera* was reidentified as *O. aenescens* by Maa (1962). During the summer months when large numbers of sea birds are nesting on the island, this species can be seen flying about and may be caught easily by sweeping with an insect net.

The specimen collected from a rabbit is certainly an example of straggling which probably resulted from the close association of rabbits and birds on the island. The fate of adult flies during the winter months when sea birds are absent from the island is unknown.

SIPHONAPTERA

PULICIDAE

Ctenocephalides felis felis (Bouché)

3 ♂ ♂, 2 ♀ ♀, ex *Oryctolagus cuniculus,* Aug. 31, 1961

80 ♂ ♂, 114 ♀ ♀, ex *Oryctolagus cuniculus,* Feb. 29, 1964

C. f. felis seldom has been reported from *O. cuniculus,* and the only records of which we are aware are those of Cable (1943), Seddon (1947), Hopkins and Rothschild (1953), Mykytowycz (1957), and Smit (1957). The last author lists the occurrence on *O. cuniculus* in England as accidental. Mead-Briggs (1961; 1963) examined over 53,000 fleas collected from rabbits in England without finding *C. f. felis.*

Of the 13 rabbits collected on Manana, 8 were examined for ectoparasites. Conditions were such that it was impossible to collect all of the fleas seen and it is estimated that only about one-third of those on the 8 animals were collected. Cat fleas were very common on the body but were found only rarely on the head of the rabbits. The greatest concentrations were on the back of the neck.

The finding of large numbers of cat fleas on rabbits on Manana indicates this species is capable of maintaining itself on this host under certain conditions. This is the first recorded instance of a naturally occurring population of *C. f. felis* on feral *O. cuniculus.* The flea could have been introduced to Manana on the rabbits or at various times by dogs or cats brought ashore by fishermen.

The *C. f. felis* from Manana might be a suitable strain for laboratory culture inasmuch as its host, the rabbit, is more convenient to maintain than other hosts. Dogs or cats have been used (Smith and Eddy, 1954; Hudson and Prince, 1958) but necessitate more care and space than would rabbits. Attempts have been made to rear cat fleas on laboratory and wild

rats and mice; however, none has been successful (Elbel, 1951; Wang, 1960; Kir'yakova, 1961; Haas, 1966).

Echidnophaga gallinacea (Westwood)

1 ♂, 35 ♀♀, ex *Oryctolagus cuniculus,* Aug. 31, 1961

94 ♂♂, 289 ♀♀, ex *Oryctolagus cuniculus,* Feb. 29, 1964

The stick-tight flea has been reported previously from *O. cuniculus* in Australia (Seddon, 1947; Hopkins and Rothschild, 1953; Mykytowycz, 1957). On Manana this flea was found in clusters of 10–12 on the upper eyelids of some rabbits and singly inside the ears of others. Most of the fleas came from the heads of freshly shot rabbits.

E. gallinacea is primarily a bird flea although it has been reported from many mammalian hosts, from some in sufficient numbers and frequency to suggest that the mammals are true hosts. It seldom has been reported from *O. cuniculus;* however, the strain on Manana obviously has adjusted to this host. It could have been introduced to the island on rabbits or by transient passerine birds.

Xenopsylla cheopis (Rothschild)

6 ♂♂, 5 ♀♀, ex *Mus musculus,* Feb. 29–Mar. 1, 1964

1 ♀, ex *Oryctolagus cuniculus,* Feb. 29, 1964

The collection of *X. cheopis* from house mice on Manana was unexpected because this flea is primarily an ectoparasite of *Rattus* sp., which do not occur on the island. The six mice had a flea index of 1.83, much higher than the index of 0.16 (average) reported by Eskey (1934) for mice trapped on Oahu, Maui, and Hawaii.

X. cheopis could have been introduced to Manana on mice, or on rats which later became extinct, forcing the fleas to survive on mice or perish. It is apparent that the mouse and the Oriental rat flea have established a compatible host-parasite relationship on Manana.

The specimen collected from a rabbit may be considered a straggler. This example is not surprising because the mice and rabbits are confined to a small area and mice can easily enter the burrows of rabbits. Cable (1943) recorded this species infesting confined albino rabbits.

MALLOPHAGA

MENOPONIDAE

Austromenopon paululum (Kellogg and Chapman) sens. lat.

1 ♀, ex *Puffinus nativitatis,* July 17, 1963

Austromenopon sp.

2 ♀♀, 1 N, ex *Sterna fuscata,* July 17, 1963

Austromenopon sp.

4 ♀♀, 1 N, ex *Anous stolidus,* July 17, 1963

PHILOPTERIDAE

Quadraceps birostris (Giebel)

1 ♂, 3 ♀♀, ex *Sterna fuscata,* July 17, 1963

Trabeculus hexacon (Waterson) sens. lat.

1 ♂, ex *Puffinus nativitatis,* July 17, 1963

Mallophaga spend their entire lives on the host, and their geographic distribution generally coincides with that of the host. For this reason factors limiting the distribution of other ectoparasites seldom are important to the Mallophaga.

Q. birostris has been reported under the name *Nirmus gloriosus* from Laysan in the Hawaiian chain (Kellogg and Paine, 1910).

METASTIGMATA

ARGASIDAE

Ornithodoros capensis Neumann

7 ♂♂, 2 ♀♀, from under rocks, Mar. 30, 1963

O. capensis is confined to sea birds and has a world-wide distribution. Studies have revealed *O. capensis* to be a complex of two species which are identifiable with certainty only in the larval stage (Kohls et al., 1965). The above record is considered in the broad sense of the species.

Kohls et al. (1965) recently listed one larva of this species from Manana. This was collected from *Anous stolidus* on November 24, 1946 by L. Kartman. It and the following species were among the specimens Kohls (1957) listed as "off terns on islands near Oahu . . ." (Kohls, personal communication).

Ornithodoros denmarki Kohls, Sonenshine and Clifford

This species is listed from Manana on the basis of two larvae recorded by Kohls et al. (1965) with the same data as the one larva listed for *O. capensis.*

A new virus has been found recently in this species, giving it added importance as a potential disease vector (Hughes et al., 1964; Philip, 1965).

PROSTIGMATA

CHEYLETIDAE

Cheyletiella parasitivorax (Mégnin)

1 ♀, ex *Oryctolagus cuniculus,* Feb. 29, 1964

C. parasitivorax is found on leporids throughout the world and has been reported from this host in the wild. According to some authorities this mite is a predator on Listrophoridae rather than a parasite of the rabbit. It was not known from Hawaii prior to its discovery on Manana.

ASTIGMATA

LISTROPHORIDAE

Listrophorus gibbus Pagenstecher

1 ♂, 13 ♀♀, 3 NN, ex *Oryctolagus cuniculus,* Feb. 29, 1964

This species is a common parasite of both wild and domestic *O. cuniculus* and has been reported from many parts of the world. This is the first record of its occurrence in Hawaii.

Listrophorus musculus Wilson and Lawrence

3 ♂♂, 10 ♀♀, 1 N, ex *Mus musculus,* Feb. 29–Mar. 1, 1964

Hawaii is the only known locality for this fur mite. It is remarkable that an animal so common and widespread as the house mouse, and probably examined as frequently as any other rodent for ectoparasites, should be host to such a restricted and, until recently, undescribed mite. It is very common on *Mus* in Hawaii and has been reported from Honolulu, Oahu and Honokaa and Kukuihaele, Hawaii (Joyce, 1959; Wilson and Lawrence, 1967).

PSOROPTIDAE

Myocoptes musculinus (Koch)

4 ♂♂, 14 ♀♀, ex *Mus musculus,* Feb. 29–Mar. 1, 1964

M. musculinus is a common parasite of wild and laboratory mice throughout the world and has been reported from Hawaii by Joyce (1957). It is more abundant on mice on Manana than the few specimens indicate; however, because of its small size and the condition of the hosts when examined it was difficult to estimate the degree of infestation.

ENDOPARASITES

While no endoparasites were identified specifically from 2 rabbits examined in August 1961, or from 13 in February 1964, it seems desirable to report the procedures used and findings made. Cursory examination of viscera revealed no nematodes, trematodes, or cestodes. Rectal pellets preserved in alcohol, and dry fecal pellets collected from the ground, proved unsatisfactory for the determination of coccidial oöcysts or helminth ova. Distorted cyst-like objects were present and additional effort should be made to identify them from new material. Rectal or freshly defecated pellets exposed to air for three days before fixation in dilute formalin (but kept damp to allow sporulation of coccidia), should provide suitable study samples. Sieving and microscopic search of intestinal contents, and similar critical examination of the blood, gall bladder, liver, and other organs, is recommended for a complete appraisal of rabbit endoparasites. There are several definitive studies of the internal parasites of the European rabbit (Bull, 1958; 1960; 1964) which can be applied directly to the situation on Manana.

The 6 mice likewise were negative for endoparasites and further attention should be paid to this species.

DISCUSSION

It is of primary significance that the sea birds, rabbits, and vegetation of Manana have reached an obvious degree of mutual ecological adjustment. The unknown original vegetation undoubtedly suffered greatly soon after it was exposed to rabbits, and events in its change to the present complex may have unfolded as follows. The large rabbit population present at the time of the brief early record of Manana (Anon., 1901) probably existed at most about

10–15 years after establishment of rabbits. This great number of animals almost certainly was generated and sustained by an original reserve of woody shrubs and creepers, and other plants. Such species as *Scaevola taccada* and *Ipomoea pes-caprae* that are common on similar offshore islets (e.g., Mokulua) reasonably could be expected to have occurred on Manana. Their absence from the more than 35-year record of plants on Manana may well be a result of their extermination and subsequent exclusion by rabbits. Parallel conditions of depletion have been observed on Laysan and Lisianski (Watson, 1961). Perhaps on Manana the pattern of destruction was modified and prolonged by a heavy bag of rabbits taken periodically for meat, annual seasonal recovery of the vegetation, and a series of unusually wet years. Whatever the details, the result is what we see today, a reasonable equilibrium between a low to moderately dense rabbit population and vegetation composed predominantly of hardy introduced grasses and forbs.

Rainfall at Makapuu Point, Oahu, 2.4 km from Manana, averages 597 mm per year (U.S. Weather Bureau, 1964), close to the 635 mm estimated for the open ocean in this region (Blumenstock, 1961), and is therefore useful as a reference to precipitation on Manana. Of the annual rainfall 77% falls between October and March, and so the April-to-September period is typically arid. Watson (1961) has suggested that on islands with rainfall regimes such as this, periodic (normally annual) droughts result in a drastic reduction of the rabbit population, which enables the vegetation to, "recover sufficiently to survive." The present annual cycle seems to be as follows. During the dry season (summer) the vegetation dies back, and the rabbit population declines considerably. Seeds have been produced and are present on the ground. When the rainy season begins (early winter), the seeds germinate, seedlings become established, and regrowth of perennials occurs before the rabbit population increases. In the winter an adequate food supply is available, but onset of the next dry season results in a return to conditions of food shortage and decline in numbers of rabbits. Drought, accompanied by recession of the vegetation, may be the strongest limiting factor for this population. However, the European rabbit does not need free water to drink and by remaining deep in its burrows in the heat of the day it minimizes transpiration loss. In pen experiments on water deprivation, rigid selection occurs, but a few rabbits survive (Hayward, 1961). The strain on Manana may have faced drastic drought conditions several times in the long period of its adaptation and may be capable of behavior resembling estivation.

In the three wet seasons of October to March, from 1961 through 1964, rainfall was normal or above normal. There were no winter droughts. These conditions support the likelihood that there was a regular November-to-April breeding season during these three years as derived from age classification of 12 rabbits collected in 1964. The driest period was June through September 1963 when only 38 mm of rain fell (half of the normal for these months), and the wettest was in March through May 1963 when 866 mm fell (five times normal). Because of the rapid percolation of water through volcanic soils and the high rate of evaporation at the latitude of Hawaii, repeated moderate rains are ideal for normal growth of most plants on Manana. Distribution of rainfall in time, therefore, may be more important than total precipitation for any year.

In addition to their effective control of the vegetation by grazing, rabbits are capable of contributing to seed dispersal. Several animals had plant reproductive structures entangled in their pelage. Thorough combing of one skin yielded many spikelets with subtending bristles from *Setaria verticillata,* some spikelets of *Cenchrus echinatus,* and one spikelet of *Chloris inflata.* Rabbits must disseminate plants from one part of the island to another, but, because of the small area, other means of transport also could account for the fairly uniform distribution of plant species.

Because our study has been limited to a review of the scanty history of conditions on Manana, brief sampling of the present flora and fauna, and interpretations of the few data available to us, we are not in a position to make a final judgment on what management practices should be adopted. It is apparent immediately, however, that Manana does support a great many nesting oceanic birds each year in the presence of rabbits. We concur with Richardson and Fisher (1950) that bird-rabbit

relationships do not seem particularly significant, but we hasten to add that this may be because they have never been probed deeply. For instance, it is conceivable that the rabbits affect the vegetation in such a way that favorable conditions for nesting by certain birds are maintained. Nesting colonies of Sooty Terns, which one of us (Lamoureux) has observed on several of the Leeward Hawaiian Islands, tend to be in more open areas covered with grasses and low herbs, rather than in areas covered with shrubs. It is quite possible that the presence of the rabbit on Manana contributes to the relative scarcity of shrubs there. In turn, the selective development of the rabbit strain on Manana may have been guided by a vegetation richly fertilized with bird guano, infusing in it a vitality sufficient to permit at least a bare survival of the rabbits in times of crisis. Without question, the ecology of birds, rabbits, and vegetation on Manana is complex, and very likely there are key interdependencies not realized at this time.

A decision now to eliminate rabbits because of some presumed interference with nesting of birds would be premature. We recommend, instead, an intensive program of ecological study to embrace particularly birds, rabbits, and vegetation. Because of the unique relationships observed between some species of ectoparasites and birds and mammals, careful attention should be paid to all of the fauna. The following immediate suggestions are made for projects that would lead gradually to an understanding of the island's more prominent ecological relationships.

1. Construction of a 20 $\times$ 50 m (open) and several 2 $\times$ 2 m (covered) exclosures to test the responses of vegetation in the absence of rabbits and the presence of birds only, and in the absence of both.

2. Establishment of permanent vegetation transect points and periodic recording of vegetation changes by photographic and other means.

3. Monthly or quarterly population estimates of birds, rabbits, and mice, with particular regard to season of year and condition of vegetation. The mark and release of trapped mammals would allow access to information on age composition, nutritional condition, reproductive cycles, and ectoparasite infestation of the populations.

4. Behavioral studies of rabbits and birds, with particular attention to social relationships of rabbits to surface- and burrow-nesting birds.

5. Study of energy relationships to determine the degree of dependence of the vegetation, and hence the rabbits, upon bird guano as a primary nutritive source.

The possible importance of the rabbit strain on Manana as an experimental animal in particular problems of medical or biological research should not be overlooked (Thomsen and Evans, 1964), and a thorough study of the population as it is related to other populations of the species in Hawaii and in the world is a need of special significance.

Further intentional introduction to Manana of organisms of any sort in the near future is not recommended. Ecological studies should be carried out with as little disturbance as possible of the present biota. The ecosystem on Manana has much scientific potential in its present condition and is within easy reach of the intellectual center of the state. This value will increase in time and in proportion to the effort made to understand and interpret this singular Hawaiian resource.

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